

Assortative Mating and Selection

in

Drosophila melanogaster.

by

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I AIMS

(a) To compare the relative effectiveness of assortative and random mating in a population under selection.

(b) To compare the relative effectiveness of selection on an index of family and individual phenotypes in conjunction with assortative and random matings with that of selection and mating on individual phenotypes.

II INTRODUCTION

(a) General.

Experimental and theoretical studies of selection have usually been concerned with selection in conjunction with random mating though some interest has been shown in the use of inbreeding with selection (e.g. Lerner, 1950).

Recently two studies have drawn attention to the possibility of an improved effectiveness of selection by the use of positive phenotypic assortative mating with selection (Breeze, 1956; James and McBride, 1958). This suggestion is further supported by Reeve (1953) who showed that the effect of assortative mating was to increase the variance between mid-parental values and thus to increase the variance between offspring family means. This places assortative mating in a category analogous to most of the aids to selection used in animal breeding since these, by weighting family means, give an increased effective variance between family means.

It does not appear to be generally recognised that selection is an inbreeding process, the intensity of which is governed by the relative

sizes of the between and within family variances and the selection differential. Nevertheless the so-called "genetic" history studies of breeds of domestic animals (e.g.) Yoder & Lush (1937). Willham (1937) and Lush & Anderson (1939) and particularly the pedigree studies made of closed populations under selection (Lerner & Hazel, 1947) have shown clearly the effectiveness of selection in the elimination of pedigrees leading to most individuals used a few generations previously. Lerner (1950), p. 180, discussing this phenomenon wrote, "Family selection, rather than selection on an individual basis is responsible for the rapid elimination of ancestors. The consequences are rather difficult to assess precisely. It may only be concluded at this point that chance must play a reasonably significant role in the process under discussion even though its effects do not seem to be reflected in the computed gains". James and McBride (1958) on the other hand accepted that selection would give rise to changes in the proportion of genes in a population derived from different ancestors and pointed out that these changes would be largely regular, irregular changes arising from the effects of chance, non-additive genetic variation and different aims of selection at different times.

In a study of the spread of genes from foundation members of a poultry flock under selection, they showed that three of the foundation sires contributed 36% of the genes in the flock four years later and that a further 10% of the genes came from a single female which was mated to one of these cocks. They showed further that this spread of genes from foundation males was 75% determined by the best estimate of their genotypes; thus the inbreeding effect seemed to be an integral part of the process of selection.

Probably selection may be looked at as a continuing migration pattern within the selected population. Each generation the genes of superior ancestors are spread more widely by the use of their superior offspring. This process may be traced for a few generations by the use of pedigrees after which each member of a generation will be descendants of the same array of ancestors so that further changes cannot be detected.

Since assortative mating involves pairing between extreme males and females and a greater differentiation between the progeny families, the intensity of this migration, or spread of genes, pattern is potentially increased.

Rendel & Robertson (1951) effectively drew attention to this migration process in their division of the selective processes from generation into the selection of males to breed males, males to breed females, females to breed males and females to breed females. Even if random mating occurred within these two levels of selected animals of each sex, a positive correlation between mates, that is, assortative mating would occur among the parents of female progeny. The migration pattern in such a selection is evident from the fact that the best males and females would leave sons and daughters while the second selected class would leave only daughters.

Since anything which increases the variance between families should increase the inbreeding effect of selection, assortative mating, and for that matter any type of family selection should increase the rate of inbreeding during selection.

In any comparison between the use of assortative mating and random mating, in selected populations, one would expect that the greater the accuracy of the assortative mating genetically, the greater would be the

difference, if any, between the response to selection under the two systems.

One method of obtaining estimates of individuals' genotypes which are more accurate than the individuals' own phenotypes is the use of an index which takes into account the family mean as well as the individuals' own phenotype. The use of such an index is commonly recommended in animal breeding as an aid to selection (e.g. Lush, 1945; Lerner, 1950). Thus one would expect that the use of such an index would give rise to a greater response to selection, a more efficient assortative mating genetically and a high level of inbreeding.

(b) Selection.

A number of long term selection experiments using Drosophila melanogaster have been carried out in recent years. Mather & Harrison (1949) selected for abdominal chaetae from the F_2 of a cross between an inbred line and a mass cultured line using a small population size, four males and four females per generation and a selection intensity of one in ten. Clayton et al (1958) selected flies of this species for the same character from a large stable base population using a population size of 20 of each sex each generation and a variety of selection intensities with the maximum being one in five. The significant feature of both of these experiments was that a steady response to selection was obtained for about 20 generations in the high chaetae number lines, after which the response to selection ceased. Mather & Harrison (1949) obtained further responses to selection at later stages in three of their lines though this was always preceded by a long period of stability. This period of failure to respond to selection was also observed by Clayton & Robertson (1957) who carried five high selection lines to from 32 to 34 generations.

Similar results were also obtained by Robertson & Reeve (1952) for thorax length in one strain and wing length in two strains of this species. In none of these cases were detailed pedigrees kept.

This picture of a response to selection for approximately twenty generations followed by a period of stability seems then to be a general one. Thus in any selection programme we are concerned with these two features, the response to selection and the level of the "plateau".

Basically the response and "plateau" in any line under selection will be determined by the sample of genetic material available in the base population and any losses occurring during selection. In the base population, the potential of a line will be affected by the number of genes, the magnitude of their effects, their frequency, their relationship with other fitness characters and their linkage relationships with other genes of positive and negative effects.

In an animal improvement problem, we are concerned with sampling adequately all of the potentially useful genetic material in the population or even the species. In a selection programme concerned with investigating differences between treatments we are only concerned with ensuring that from any given base population, the sampling of lines for different treatment is relatively unaffected in both response and "plateau" level by the choice of different samples from such a foundation.

Similarly, since population size may affect both the rate of response to selection (after the initial generations) and the level of the "plateau" if the inbreeding loss of variability is appreciable, the actual population sizes in any lines receiving different treatment should be equal. It has been pointed out above that this does not mean that such lines would have

equal effective population sizes; in fact, the effect of various treatments on the relationship between actual and effective population sizes is of some interest in selection studies.

An alternative approach to this problem of base population sampling for selection treatment comparisons was that of Clayton et al (1957) who used five replicates in each treatment. They also stabilised the actual population size during selection by selecting 20 pairs out of 25, 50, 75 and 100 measured pairs in their different treatments. Since these were mass mated, there was no direct information available on the effective population sizes in these four selection intensity treatments.

If assortative mating affects the effective population size by increasing the rate of inbreeding, one might expect that a more intense inbreeding would cause a greater degree of fixation of genes during selection. If minus genes affecting bristles were fixed in lines because of a greater rate of inbreeding, one might expect that the more rapid response to selection in any comparison might be associated with a lower plateau. Some evidence of this type may be found in the "Monte Carlo" type of selection experiments involving different intensities of selection. (Cockerham & Martin, 1958).

(c) Assortative Mating.

Assortative mating has been a relatively neglected field of study in quantitative inheritance. Further, where studies have been made, different workers have given slightly different meanings to the term assortative mating. No work has been carried out on the use of assortative mating in conjunction with directional selection. Wright (1921) used

path coefficients to study the effects of mating an unselected population assortatively. He dealt with the problem in terms of the number of genes affecting the character and his conclusions were that assortative mating would give rise to an increased variability in the population, ^{and} some increase in homozygosis when the number of genes was small and the correlation between mates was nearly perfect. The small increase in homozygosis arose because some of the genetic correlation between mates was due to alleles within a locus and some to genes with similar effects at different loci. The genetic correlation achieved between mate (m) was shown to be equal to $r_{SD}h^2$ where r_{SD} is the phenotypic correlation between mates and h^2 is the heritability. Under his conditions of mating an unselected population assortatively over a number of generations, the increase in variation was large since at the extremes of the phenotypic range there is effectively selection in both directions. A value of $m = 0.5$ would be sufficient under those conditions to reach a genetic variance at equilibrium identical with that of the limiting inbreeding value of $F = 1.0$ when the genetic variance would have increased to $2\sigma_G^2$ (F is the coefficient of inbreeding). Higher values of m under these conditions would allow still greater variability at equilibrium though extremely high values of m are, in practice, difficult to obtain.

This increased variance between families in a population is the result of a greater variance between midparental means and the effect is largely achieved in the first or second generation of assortative mating.

Reeve (1953) showed that one consequence of this increased midparental variance and between progeny family variance was that, for a

model involving additive gene action, estimates of heritability with low error variance could be obtained from parent offspring regressions. He used the term assortative mating in two senses, the first involved the mating of an unselected group of males and females assortatively and the second involved the choice of parents (as opposed to selection) to ensure a wide range of midparental values. This latter method gave relatively sensitive heritability estimates thus reducing the amount of labour in this type of routine study.

Breeze (1956) extended this examination of the effects of assortative mating, again for a model without selection, to a consideration of the additive and nonadditive components of genetic variation. He used the technique of Mather (1949) to subdivide the variation in a quantitative character into fractions due to the additive or fixable component, a component due to dominance deviations and a fraction due to non-heritable variation (D, H and E respectively).

He seems to have been the first to realise the significance of the increase in the genetic variance between families as a potential tool in animal and plant selection. The same conclusion was reached by James and McBride (1958) from quite a different type of evidence. They found that the spread of genes from female ancestors in a poultry flock under selection was determined more by the breeding value of the male to which they were mated than by their own breeding values, apparently due to the better identification of the breeding values of males than females in poultry.

To date, no theoretical study has been made of the combined effects of selection and assortative mating. This is not surprising

in view of the complexity of the problem even under relatively simple assumptions about the nature of the genetic variation. Such assumptions are not likely to be valid after the first few generations of selection even for relatively simply inherited characters as sternital chactae number in Drosophila melanogaster (Clayton et al, 1958).

A preliminary comparison (unpublished) was made between the effects of positive and negative assortative mating and random mating to provide evidence upon the change in the variability in sternital bristle score (4th and 5th segments) in Drosophila melanogaster under these mating systems. Three lines were drawn from a single group of 10 full sib families and an identical pattern of rotational mating was practised in each line so that the pedigrees of the families in each line in each generation appeared identical and led back to the same original sib families in the same way. Because of this form of standardising the descent from the base population, the assortment, positive and negative, was practised on a within family basis, that is, using only one half of the genetic variation. No selection was practised and no replicates were kept.

The within generation analysis of variance for nine generations is shown in Table 1.

Table 1. A comparison of variances and intraclass correlations from three systems of mating (sternital chactae).

	Between full sib family Component.	Total variance	Full sib correlation
Assortative mating - +ve	5.53	12.77	0.434 ± 0.158
Random mating	3.01	11.55	0.261 ± 0.068
Assortative mating - ve	1.73	10.24	0.169 ± 0.0483

While the differences in total variance were not significant they suggested that total variances may be affected by assortative mating and in a selection programme this would give rise to increased selection differentials. The differences in family components of variability and full sib correlations supported the suggestion of Breeze (1956) that the use of assortative mating may prove a valuable aid to selection.

d. The Experiment.

In the absence of a theoretical examination of the effects of assortative mating with selection, it was decided to compare assortative with random mating in a selection experiment for abdominal chaetae (4th and 5th sternites) in Drosophila melanogaster.

The comparisons were made in pairs, each derived from a single base population, sampled to reduce the effect of the base population on the subsequent behaviour of the selected line. The method of sampling is described below (3b).

Within any pair of lines, an attempt was made to keep selected population sizes the same by the preparation of reserve matings in each generation.

Two comparisons were made based upon selection and assortative mating on individual phenotype (mass selection with and without a correlation between mates). A third comparison was made using an index of family and individual merit (Lush, 1947) as the basis for selection and assortative mating. Since no experimental evidence was available on the effectiveness of selection on such an index, the experiment made a comparison between index and individual selection possible. In this

comparison, however, a single base population was not used so that the sensitivity of the comparison may have been lowered.

Because a higher rate of inbreeding was expected with index selection, it was decided to use a larger population size, twenty full sib families of ten males and ten females compared with ten full sib families in the other comparisons.

The work on selection in Drosophila melanogaster of Mather and Harrison (1948) and Clayton and Robertson (1957) on this character and of Robertson & Reeve (1952) on wing and thorax length suggested that the "plateau" phase of selection should be readily recognised. It was therefore decided to continue the selected lines until this stage was reached. Differences in the level at which response ceased might be expected in lines drawn from a similar base population by chance or if the use of assortative mating gives rise to greater inbreeding during selection.

IV Material and Methods

(a) The Stocks.

The Kaduna strain of Drosophila melanogaster was used in these experiments. The detailed history of this strain has been adequately described by Clayton et al (1956). Briefly the strain has been maintained at 25°C at a size of approximately 5000 since 1949. Thus roughly 130 generations of random breeding had occurred under these conditions before flies were sampled for this study.

Three separate samples were taken at different times from the Kaduna cage to form base populations for the O, D and F lines.

(b) The O Lines.

The O or original sample was divided into full sib families and inbred slightly for 2 generations to a coefficient of 0.1 (actually 0.0922).

From ten full sib families, each of ten males and 10 females, a selection of the 20 males and 20 females with highest sternital bristle scores was made. This selection was divided so that the full sib families from which the selected flies were drawn were approximately equally represented in each half and an equal selection differential was achieved in each half.

This form of sampling two lines from a single base population represented an attempt to minimise differences in the subsequent behaviour of the two lines under selection due to slight differences in the base population sample.

One half was mated assortatively to give the ASO line and the other half of the selected group was mated at random to give the RSO line. Each generation ten males and ten females were scored from each of ten full sib families and selections were made to provide for 10 pair matings in the following generation. Thus a selection intensity of $1/10$ was attempted.

All selection in all lines was practised on chaeta score on the 4th and 5th abdominal sternites.

In order to ensure that ten successful matings were available, spare matings were made up each generation. By generation twelve losses of matings had become so heavy and regular that the total number of matings made in each generation had reached 30, i.e. twenty reserve matings were

available in each line for the remainder of the experiment. Though the loss of two thirds of the matings seldom occurred, loss of 50% of the top twenty matings was common after generation ten.

With assortative mating, this loss of matings did not seriously affect the correlation between mates since the whole thirty males and females were mated assortatively. In the random mated lines, however, the top 15 males and females were mated at random and the remainder provided another random mating level. Thus, if a loss of matings in the top 15 caused individuals of the second level to be used, a positive correlation between mates would be generated. If the loss of matings was particularly low, this method of dealing with the random mating lines led to a slight loss of selection intensity because the first ten matings would not necessarily represent the highest ten males and females since the first random mating level included the best 15 males and females.

(c) The D Lines.

Ten pair matings were made up from flies hatching from a sample of eggs taken from Kaduna cage to provide the base generation for the D or duplicate lines. Ten males and ten females were scored from each and a selection of the highest scoring twenty males and females was made. This selected group was divided in half so as to give equal representation of each of the full sib families in each line. The assortatively mated group became the A.S.D. line and the random mated line became the R.S.D.

The two D lines were started at the same time as the O lines and the treatment of the two pairs of lines was identical in all respects.

(d) The F Lines.

The F, or family selected lines were established when the O and D lines had reached generation 8, from twenty progeny groups taken from fertilized females sampled from the Kaduna cage. Ten males and ten females were scored from each family and 40 males and 40 females were selected on the basis of an index of family and individual merit (sternal bristle score). This selected group was divided in the manner described for the O and D lines to form the AFIS (assortatively mated family plus individual selected line) and the RFIS (random mated).

The index used was of the type (Lush, 1945)

$$I = P + W_{fa} P_{fa}$$

where P is the individual's phenotype, P_{fa} , the family average (both in terms of deviations from the generation mean and W_{fa} is a weighting factor.

Lush (1947) provided a solution for the value of W_{fa} which gave a maximum correlation between an individual's genotype and the index value. His expression for W_{fa} is given as

$$W_{fa} = \frac{n}{1 + (n-1)t} \frac{r^G - t}{1 - r^G}$$

where n is the family size, r^G is the relationship between members of the family and t is the phenotypic correlation between members of a family, that is,

$$t = r_h^G + c^2.$$

Using the estimate of 0.52 for the heritability of this character in the Kaduna population (Clayton et al, 1959) and their value of 0.03 for c^2 , t for full sib families is 0.29 and for families of size 10, $W_{fa} = 1.16$.

Since Dempster & Lerner (1947) showed that the use of the exact

value for W_{fa} is not critical, it was decided to use the operationally more convenient W_{fa} value of 1.0. Such a drop in value could, in fact, be justified by the fact that in most generations, many of the families scored were related.

The use of this type of index was shown by Lush (1947) to increase the response to selection (ΔG) in the ratio.

$$\frac{\Delta G_{fa} + i}{\Delta G_1} = 1 + \frac{(n-1)(r^G - t)^2}{(1-t)[1 + (n-1)t]}$$

Substituting in this equation gives the ratio 1.075, that is, selection on the index should give approximately 7.5% greater response per generation.

Since the index value represents a better estimate of the genotype than an individual's phenotypic score, mating assortatively on index values should be more effective than sample phenotypic assortative mating as in the O and D lines.

The sexes were selected separately on the same index using deviations from the sex mean. For convenience, the family mean deviation from the generation sex mean was added to the scores of the individuals of the family. The index used was thus

$$I = \bar{P} + P + W_{fa}P_{fa}$$

where \bar{P} is the generation sex mean and P and P_{fa} are individual and family deviations from \bar{P} . $W_{fa} = 1.0$.

In the F lines as in the O and D lines, spare matings were maintained to ensure that twenty families were available for scoring each generation. From generation 7 onward, a total of 50 matings were made up in each line each generation.

In all lines, all matings were made up on fresh food on the one

day and the generation interval was approximately three weeks.

Since full pedigrees were available in all lines, inbreeding coefficients for each family could be computed and average inbreeding levels for each generation obtained. The technique used for computing inbreeding was that described by Cruden (1949) and Emik & Terrill (1949).

(e) Summary of selected lines.

ASO Assortative mated selection line, O (original) base population.

RSO Random mated selection line, O (original) base population.

ASD Assortative mated selection line, D (duplicate) base population.

RSD Random mated selection line, D (duplicate) base population.

AFIS Assortative mated, family plus individual index selected and mated line.

RFIS Random mated, family plus individual index selected, and mated line.

The intensity of selection in lines ASO, RSO, ASD and RSD was 10 pairs/100 pairs while in AFIS and RFIS it was 20 pairs/200 pairs, that is 1/10 selection intensity in all lines.

IV Results

(a) Base populations.

Within pairs of treatments, some indication may be obtained of the efficiency of two lines sampling for minimum differences in two ways. The first is to examine the two populations after a few generations to determine the contribution made by each of the original families to each line. The second would be to cross the two lines at the end of the experiment and select from the cross.

Both of these techniques were used in these experiments though the second will be discussed later.

The first method uses the method of James & McBride (1958) to determine the percentage of the genes in each pair of lines at generation four derived from each family scored in the base generation.

The results of this pedigree study are shown in Table 2.

(b) Response to Selection.

The responses to selection per generation in lines ASO, RSO, ASD, and RSD are shown in Figure 1. The same responses in terms of the cumulative selection differentials applied are shown in Figure 2 since this comparison gives a more realistic picture of what occurred in the lines, both in terms of the total amount of selection differential achieved in the different lines and the associated response. The use of this base enables a representation to be given of the response to be expected for different values of the heritability. Though these expected responses for two values of the heritability are plotted linearly, the effect of inbreeding in the different lines will cause the expected response to be curvilinear and different for each line.

Figure 3 shows the response obtained in the F lines, per generation, per cumulative phenotypic selection differential and per cumulative index selection differential. Once again the expected response for an individual heritability of 0.52 is shown. The responses in Figures 1, 2 and 3 are all given in terms of the means of the two sexes each generation. Since the ratio of male chactae number to female number changed in some of the lines, these ratios for each line are presented in Figure 4.

Table 2. The percentage of genes in each line at generation 4 derived from families in the base population.

O Base population Families		1	2	3	4	5	6	7	8	9	10
% age genes	ASO	0	0.63	0	0	45.0	11.25	13.75	6.88	0	22.5
	RSO	0	3.13	0	0	36.88	1.25	45.63	0	0	13.13
B Base population Families		1	2	3	4	5	6	7	8	9	10
% age genes	ASD	16.88	0	16.88	0	0	0	21.88	8.13	33.13	3.13
	RSD	20.63	0	15.63	16.88	0	0	29.38	0	0	17.5
F Base population Families		1	2	3	4	5	6	7	8	9	10
% age genes	AFIS	0	0	0	1.56	1.56	0	0	45.3	50.0	1.56
	RFIS	10.94	0	0	0	0	0	0	8.44	34.38	31.56
F Base population Families		11	12	13	14	15	16	17	18	19	20
% age genes	AFIS	0	0	0	0	0	0	0	0	0	0
	RFIS	0	4.69	2.5	0.94	0	0	6.56	0	0	0

During the experiment the selection differentials achieved and used in Figures 2 and 3 for response comparisons were in most cases less than those attempted, due to a loss of matings. To some extent, this loss of matings would be due to chance as for example, when a fly becomes stuck onto the fresh medium. Since, however the selection differential is concerned with the average of the selected group, such a loss would not have altered the average of the remainder though this average would have been slightly lowered by the inclusion of spare matings. The loss of selected matings became increasingly severe in most of the lines after the first few generations and it is difficult to escape the conclusion that this loss was due to natural selection opposing artificial selection. This was particularly noticeable in the assortatively mated lines where the ranked matings were numbered consecutively. There it was consistently found that the loss was heavier in the first half of the matings than in the second half. The differences between the attempted and achieved selection differential are apparent from Figure 5. It can be seen that the difference tends to increase throughout the period of selection in all lines. The extremely low selection differential in generation 13 of line AFIS was the result of an accident. The selected flies of this generation were mixed. Since only the lowest selected flies in each family could be identified these alone were used to produce generation 14.

The very high selection differentials and accelerated rates of response in line ASD from generation 8 to 11 and in line RSD from generation 12 to 16, was the result of the appearance and fixation of a recessive gene scabrous in these lines. Line ASD was backcrossed to

Kaduna unselected flies to determine the magnitude of the effect of scabrous in different intermediate genotypes. I am indebted to Dr. Alan Robertson for the backcross results shown in Table 3. The numbers

	Wild type				Scabrous				Mean difference
	♂	♀	Mean	♂/♀ ratio	♂	♀	Mean	♂/♀ ratio	
F ₁	47.2	60.1	53.65	.785					
F ₂	45.8	62.2	54.0	.736	58.8	87.6	73.2	.671	19.2
Kaduna backcross 2 F ₂	41.2	50.7	45.95	.813	51.95	71.9	61.93	.723	15.98
Kaduna Backcross 3 F ₂	35.57	48.1	41.84	.740	51.5	73.6	62.55	.700	20.71
ASD Backcross 2	49.5	61.4	55.45	.806	59.5	88.1	73.8	.675	18.35
ASD Backcross 3	51.4	66.1	58.75	.778	68.2	97.7	82.95	.698	24.20

Table 3.

involved in those backcrosses are small since scabrous shows a low viability and the ratios obtained in F₂s of crosses between D lines and O lines differ significantly from 3:1. In 1000 flies scored from 100 families the ratio obtained was 120:880. It seems possible that scabrous flies appeared in ASD generation 15 since extreme flies of both sexes appeared in one family (Figures 5 and 6) though these flies were not checked for other manifestations of the scabrous phenotype. All

matings with flies from this family were sterile. Clayton (personal communication) found scabrous phenotypes in one of his lines selected for sternital chaetae. He found it impossible to maintain scabrous stocks from this line.

It is of interest that at the appearance of this gene occurred in the two lines at almost exactly the same mean count, approximately 58 chaetae. However, in view of the evidence of the backcrosses, it is difficult to give much credence to any theory of acceleration. Any such theory would either require that the magnitude of the scabrous increased in the presence of a high bristle background or that the scabrous effect required a certain threshold before its effect could be manifested. The backcross table discounts either suggestion.

The effect of scabrous on bristles is, nevertheless, so large that it would have immediately been noticed had it occurred in any of the previous generations and in view of the inbreeding which had already occurred (25% in ASD and 35% in RSD) it is surprising that the homozygous scabrous was never encountered. In view of its low viability, it is possible that either selection (or chance) had brought to light some other gene with slight (or no) effect on bristles itself but with the ability to render the scabrous homozygote relatively viable. It is also possible that such a change could occur by crossing over. In any event if the presence of another gene were necessary to improve the vigour of the scabrous homozygote, it would also be present in a certain proportion of the F_2 scabrous homozygotes and this would allow some to survive.

Other effects of the scabrous gene were observed on the male:

female bristle ratio (Figure 4) and on the phenotypic variance of the population (Figure 8).

It is also possible that another recessive gene of relatively large effect occurred in line ASD at generation 15-16. Certainly there was a large increase in the magnitude of the selection differential (Figure 5) the rate of response (Figure 2), phenotypic and genetic variance (Figure 8). Further evidence is available from the behaviour of the RSD line. This line stabilised after scabrous had been fixed at the level of the RSD line before generation 16.

The aims of the experiment were in no way served by the appearance of scabrous since any comparison of selection treatments involving the D lines has little value after generation 8 in ASD and generation 12 in RSD.

Analyses of variances were made within each generation in each line and in some cases significant family X sex interactions were found. The F ratios and their significance are given for this interaction in each generation in each line in Table 4.

One might expect that significant interactions might occur immediately preceeding and during any important change in the male/female bristle ratio (Figure 4) to some extent this is so though naturally interactions of a type not selected could and presumably have occurred.

(c) Variability.

The frequency distributions of the base populations, generation five, ten and fifteen are shown for each sex and each line in Figure 6. On the whole, the distributions appear to be normal though a skew may appear occasionally in the D lines and in generation 15 of

Family X Sex interaction F (variance ratio).

	ASO	RSO	ASD	RSD	AFIS	RFIS
0	1.40	1.40	1.47	1.47 x	2.38xx	2.38xxx
1	2.43x	2.15x	5.63xxx	-	1.82x	2.17x
2	-	2.19x	2.07	1.66	1.24	2.39xx
3	1.98	1.76	1.98	2.01x	1.42	1.10
4	9.97xxx	-	1.11	1.96	1.0	-
5	-	1.37	1.22	-	1.21	1.10
6	-	1.41	-	-	-	1.30
7	2.51x	1.50	1.51	1.01	1.57x	1.86x
8	2.31x	1.34	1.38	1.28	1.64x	1.01
9	2.14	-	2.32x	-	1.56x	1.23
10	-	1.26	1.11	1.08	1.50	1.05
11	2.30x	1.40		2.56x	1.58x	1.52
12	-	1.20	1.90	2.11x	4.29xxx	3.30xxx
13	1.57	-	-	4.54xxx	1.17	1.67x
14	1.84	1.08	3.04xx	1.69	-	1.10
15	-	-	2.86xx	1.61	1.26	-
16	1.82	-	1.00	-		
17	2.30x	1.22	1.81	2.16x		
18	-	-	-	1.13		

Table 4.

The F values and their significance for Family x Sex interaction variance in each generation in each line.

x Significant - P = 0.05
 xx Significant - P = 0.01
 xxx Significant - P = 0.001

the ASO line. In these cases the appearance of a number of flies with extremely high bristle counts is responsible. This type of phenomenon is generally followed by a rapid response to selection though in ASO generation 15, all of the matings involving the extreme deviants failed. Figure 7 shows the variability of the A lines and it can be seen that the high variability of ASO generation 15 is not typical.

Figures 7, 8 and 9, which show the variability of the six selected lines, were derived from within generation analyses of variance between and within full sib families. The use of the term genetic to express $2 X$ (the between family variance component) may be a little misleading in the case of the assortative mated lines since this presumably provides a biased estimate of σ_g^2 . Since the exact nature of the bias cannot be estimated for conditions of continued assortative mating with selection, it was considered desirable to present the components as genetic for comparison with the random mated lines. Similarly, the estimates of heritability in Figure 10 are derived directly from the data presented in Figures 7, 8 and 9.

Regressions of offspring on midparent for each generation in each line are shown in Table 5. It can be seen that the regressions tend to become smaller throughout the experiment.

Pooled within generation full sib intraclass correlations are shown in Table 6.

Mid Parent Regressions.

	9 df. ASO	9 df. RSO	9 df. ASD	9 df. RSD	19 df. AFIS	19 df. RFIS
	INDEX					
0-1	.292	.135	.279	.277	.584	.540
1-2	-.038	.160	-.626	-.027	.393	.574
2-3	.100	.619	.307	.184	.197	-0.89
3-4	.310	1.11	.797	.935	.475	.470
4-5	.730	1.05	.104	.310	-.150	.176
5-6	-.120	.207	.164	.702	.130	.582
6-7	.325	-.150	.296	1.543	.195	.372
7-8	.414	.044	.233	-.062	-.256	.305
8-9	-.096	.661	.418	.204	.611	.481
9-10	.497	.551	.090	.560	.210	.215
10-11	.043	.071	-	.163	.500	.415
11-12	-.012	.819	-.497	-.346	.145	.345
12-13	.487	-.303	-.478	.098	.391	.313
13-14	.848	-.121	.216	.545	-.029	.376
14-15	1.180	.403	.655	.575	-	.724
15-16	-.488	-.204	.634	.288	-.150	-.172
16-17	-.078	.250	.003	.120		
17-18	.112	-.597	.015	.343		
18-19	-.059	-.855	.083	1.096		

Table 5.

The regressions of offspring on mid-parent for each generation in each line.

	Intra class correlations.	
	Generations 1-8	8-final.
ASO	$0.123 \pm 0.031^{(1)}$	0.104 ± 0.029
RSO	0.160 ± 0.040	0.068 ± 0.019
ASD	0.140 ± 0.035	-
RSD	0.086 ± 0.024	-
AFIS	$0.172 \pm 0.033^{(2)}$	0.111 ± 0.02
RFIS	$0.145 \pm 0.028^{(3)}$	$0.068 \pm 0.018^{(4)}$

Table 6. Pooled within generation estimates of heritability.

(1) Generations 15 and 17 omitted.

(2) Generation 5 omitted.

(3) Generation 4 omitted.

(4) Generation 15 omitted.

(Generations omitted from analysis on grounds of non-orthogonality or abnormal variances or both).

(d) Assortative mating.

In the mating programme of the assortative lines, the selected males and females were ranked from the highest to the lowest scoring and mated on rank. This meant that regardless of losses of mating, reasonably high phenotypic correlations between mates were obtained. In the random mated lines, however, apart from chance, correlations between mates could only occur by heavy losses of matings since the selected flies were always divided into two levels for random mating.

An examination of the correlations between mates shown in Table 7 reveals that, while the values obtained in the assortatively mated lines were consistently high, the values obtained in the random mated lines were generally low at first but later, as loss of matings became more important, positive correlation coefficients were achieved. Their dependance upon the loss of matings can be found by comparison with the random mating selection differential results shown in Figure 5.

The differences between assortative mating and random mating in response in each generation for each pair of lines is shown in Figure 11. The effect of the scabrous gene on the comparison involving the D lines after generation is clearly shown and it is probably desirable to ignore this difference after generation 8. The standard errors given below for the differences between lines plotted in Figure 11 are not suitable for D line comparisons beyond generation 8.

The standard errors for these differences are

AFIS - RFIS,	\pm 0.273
ASD - RSD,	\pm 0.356 (generations 0-7)
ASO - RSO,	\pm 0.379.

Table 7. Phenotypic Correlation between mates.

	ASO	RSO	ASD	RSD	AFIS	RFIS	Index AFIS	Values RFIS
0	0.923	-0.084	0.927	-0.443	0.677	0.138	0.910	0.048
1	0.869	-0.077	0.875	-0.134	0.383	0.094	0.938	0.535
2	0.919	0.100	0.847	-0.145	0.574	-0.173	0.813	-0.392
3	0.833	0.182	0.970	0.559	0.442	0.239	0.800	0.339
4	0.932	0.224	0.900	0.077	0.592	0.126	0.960	-0.044
5	0.641	0.025	0.495	0.588	0.351	0.313	0.972	0.934
6	0.853	-0.148	0.962	0.245	0.313	-0.003	0.969	0.187
7	0.963	0.152	0.757	-0.415	0.262	-0.528	0.779	-0.339
8	0.910	0.223	0.793	0.071	0.430	0.373	0.964	-0.008
9	0.940	0.490	0.897	0.066	0.836	-0.255	0.988	-0.005
10	0.956	0.600	0.451	0.425	0.617	-0.056	0.988	-0.496
11	0.982	0.436	0.932	0.616	0.504	-0.038	0.940	-0.329
12	0.972	-0.024	0.935	0.464	0.835	-0.265	0.970	-0.139
13	0.878	0.519	0.458	0.709	0.295	-0.223	-0.077	0.130
14	0.759	0.559	0.959	0.505	0.676	0.789	0.950	0.901
15	0.899	0.463	0.990	0.752	0.650	0.335	0.990	0.867
16	0.935	0.521	0.907	0.587				
17	0.868	0.105	0.977	0.934				
18	0.978	-0.029	0.965	0.508				
19								

The F line differences are significant from generation two onwards while the O and D line differences become significant from generation three and two respectively. The regularity of the F line is presumably due to the fact that 400 flies were measured each generation compared with 200 in the O and D lines.

The F line difference is significantly greater than the O line difference from generation three onward with the exception of generation 9 whereas it is only significantly greater than the D line difference in generations 3, 5 and 7 before the effect of scabrous renders the comparison invalid. The D lines difference significantly exceeds that of the O lines in generations 2, 4 and 6.

In general the results are in line with the suggestion that the effectiveness of assortative mating genetically affects the difference between assortative mating and random mating in a selection programme since the accuracy of assortative mating is greatest when based on an index. Also the preliminary inbreeding of the O lines would slightly lower the accuracy of the assortative mating at genetic level (actually the values of m expected in the assortatively mated base generation would be 0.50 for AFIS, 0.46 for ASD and 0.40 in ASO).

(e) Index Selection.

The experiments carried out allow four comparisons between index selection and individual selection though none of these comparisons are paired in the sense of the lines arising from a single base population. Two of the differences are between assortatively mated lines and the other two random mated lines. The differences are shown for each generation in Figure 12. Once again comparisons involving ASD are

only useful before generation 8 and with RSD up to generation 12. The other two line differences in Figure 12 are concerned with the differences between the D lines and the O lines since this may result from the inbred base population used in the O lines.

The standard errors of these differences are as follows:

AFIS - ASD	± 0.337	} generations 0-7.
ASD - ASO	± 0.372	
AFIS - ASO	± 0.334	
RFIS - RSD	± 0.298	} generations 0-12.
RSD - RSO	± 0.364	
RFIS - RSO	± 0.325	

The only full comparison in the assortatively mated lines is that of AFIS - ASO (significant from generation 1 onwards) and this will include not only the effect of the index selection and mating but also any effect arising from the inbred base population of the ASO line. This difference continued to rise until generation 6 after which it remained constant until the end of the experiment.

The difference AFIS-ASD (significant generation 2-7) rose irregularly until the appearance of scabrous ended the useful period of comparison.

The differences in the random mated lines between index selection (RFIS) and the two mass selected lines were all significant after generation 2 and remained so until the appearance of scabrous in RSD at generation 12. RFIS-RSD increased until generation three after which it showed no change until generation 12. RFIS - RSO rose until generation 6 after which it remained approximately constant until generation 11 after which it dropped to a new stable level until the end of the experiment.

(f) Inbreeding.

Average levels of inbreeding were computed for all lines in each generation and are shown in Figure 13. For comparison, curves showing the expected inbreeding for effective population sizes of 5, 10 and 20 pairs of flies are shown in this graph. The greatest rate of inbreeding was observed in line AFIS which had an actual population size of 20 pairs per generation. The inbreeding rate in this line was equivalent to only two pairs of flies per generation at first and an examination of Table 2 shows that 95.3% of the genes in generation 4 were derived from two families in the base population. By generation 6 this had risen to 98.3% from the pedigree study. With the exception of lines AFIS and RSO, none of the curves shown in Figure 14 were significantly non linear. The very rapid inbreeding rise in RSO during the initial generations was brought about by the appearance of a family with a mean of 5 bristles above the generation mean in generation 1. As a result, ten out of the twenty flies which were parents of generation 2 were selected from this full-sib family. The effect of such a bottleneck is to show a higher rate of increase in the average inbreeding level for several generations.

The fact that the inbreeding levels are the average F of all of the families means that, though the inbreeding coefficient in a single family may rise rapidly, it is not until the genes of that family either spread right through the population or are eliminated by selection, is the effect completed. The few cases of a drop in the average F value are the results of the elimination of a highly inbred group. The graphs illustrate well the temporary nature of such fluctuations.

If, as postulated, the selection practised is a determining factor in the level of inbreeding achieved, one would expect this to be reflected

in an association between the level of inbreeding in a family and the performance in bristle score of its members. Further, if the level of inbreeding is associated with lower vigour, then the existence of a strong positive relationship between chaeta score and inbreeding may lead to a greater loss of matings. The regressions of score on inbreeding for each generation in each line are shown in Figure 15. The average regression is positive, 0.134 chaetae per percent inbreeding.

The striking rise in size and variability of these regressions in ASD after generation 8 and in RSD after generation 12 provides an interesting example of the association between selection and inbreeding while the effects of a single gene (scabrous) are under strong selection. The larger population size in AFIS and RFIS than in the other lines makes their regression coefficients a little less variable but on the whole these regressions are difficult to interpret.

In lines like AFIS where the effective population size is considerably less than the actual population size and it is therefore possible for the effective size to be increased, it is found that negative values of these regressions are always associated with a lowering of the rate of inbreeding, suggesting that the elimination of the more inbred families which causes the lowering of the average inbreeding level was again a selective effect.

Another effect of inbreeding is shown by a comparison between the regressions in Figure 15 and the differences between expected and achieved selection differentials shown in Figure 5. When high regressions are found, there is generally a large drop in selection differential, presumably due to the lower vigour of the high-scoring, relatively more highly inbred families.

Relationships between inbreeding, chaeta score, fitness, response

and between-family variances are complex and are unlikely to be unravelled by simple comparisons.

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V. Discussion

The general impression arising from these selection comparisons is that the results are in agreement with what might have been expected from the arguments presented in the introduction. In all three comparisons, the use of assortative mating allowed an increased response to selection to be made compared with that under random mating. This additional response in all comparisons seemed to be associated with a slightly greater response per unit selection differential applied, that is, a higher heritability, and in the D and F lines a greater average selection differential. In the O lines, a number of features showed a difference from the D and F lines, and one such factor was the lower cumulative selection differential of the ASO line.

Actually the expected selection differentials were consistently higher in ASO than RSO, but from generation 8 onwards losses of selection differential in ASO (Figure 5) lowered its achieved selection differential below that of RSO. By generation 12 the cumulative achieved selection differential in RSO had surpassed that of ASO, and this position was maintained and accentuated until the end of the comparison. From generation 9, following the advent of the persistent loss of selection differential in ASO, the rate of response in ASO was lowered and the difference between the lines diminished rapidly until generation 12 (Figure 11) when losses of selection differential response made the rate of advance in the two lines approximately equal.

The rates of inbreeding in the D and F line comparisons were again as one might expect if inbreeding were associated with selection and the magnitude of the between-family variances. The greatest rate of inbreeding was achieved in the line in which family weightings (which do not show in

the between-family heritabilities of Figure 9) and assortative mating combined to increase the between family variances. Certainly the difference between the rate of inbreeding of the F lines is greater than that between that of the D lines. In the O lines again the difference was not as expected, RSO being more highly inbred than ASO. This was initially due to the appearance of an extremely high scoring family in RSO generation 1. The level of inbreeding in ASO may also have been held back by a small but consistent negative regression of score on inbreeding within generations from generation 6 to 11 and the persistent loss of selection differential in this line from generation 8 onwards; this loss increased after generation 12 when a series of high positive scores on inbreeding regressions were obtained. It should be noted that Clayton et al. (1957) did not take into account an inbreeding effect of selection in their estimate of the amount of inbreeding in their lines. This may affect their conclusion that the variance between their high selected lines was greater than one would expect from genetic drift alone.

The third feature in which the O lines disagreed with the F and D pairs was the level of plateau reached by the A and R lines respectively. AFIS and ASD ceased to respond at a higher mean score than RFIS and RSD respectively while at generation 19 ASO and RSO were not significantly different though RSO was 0.2 chaetae higher than ASO. However, after 5 generations of relaxed selection with random mating ASO was two bristles higher than RSO, and the two lines were almost identical in mean score with their position at generation 18.

If the behaviour of selected lines is determined by the base population sample and the loss during selection, one would expect that the line showing the greater rate of inbreeding would reach a plateau at the lower level, provided the base population was identical. The reverse

occurred in the F and D line comparisons. This suggests that the loss of genes during selection may not be so important where a more effective selection procedure is responsible for the higher rate of inbreeding. The alternative explanation is that in both the F and D pairs of lines the assortatively mated base populations both contained a greater potential than the randomly mated base samples. While this is certainly possible, it should be remembered that over 98% of the genes in AFIS came from two half-sib families out of twenty.

Some information on the differences between the pairs of lines at plateau is available from selected lines established from crosses within the three pairs of lines.

The F line cross was made at generation 13 and after 8 generations of selection the line selected from the cross (FF) was discontinued. Its chaeta score was 64, almost identical with AFIS when it was discontinued because of low fecundity at generation 16.

ASD was selected until generation 24, after which selection was discontinued because of low fecundity; selection was then relaxed and the line scored for another five generations with rotational matings. At generation 24 ASD had reached 90 chaetae and after two generations relaxed selection it rose to 91.5 and then fell for three generations to 88.

The line (DD) selected from a cross between ASD and RSD at generation 19 reached 91.5 after seven generations of selection and at generation 11 had reached 92.5 chaetae.

The line selected from the O line cross (OO) rose slowly for seven generations to a level two chaetae above the mean of the O lines (59.5) when discontinued at generation 19 after which it has risen steadily for another five generations to 67.5 chaetae.

Since the genes which differ in different lines should have a

frequency of approximately 0.5 after a cross, selection should be extremely effective immediately following such crosses. In spite of this the lines selected from crosses within pairs did not readily overtake the level of the higher line entering the cross. This is in contrast with the results of selection from such crosses by Mather and Harrison (1949), Robertson and Reeve (1952) and Clayton and Robertson (1958).

Results more in line with those of these workers occurred when a selected line (FO) was drawn from a cross between FF (64 chaetae) and OO (61 chaetae). This rose rapidly to 72 chaetae in three generations, after which response ceased abruptly and remained constant until generation 6.

This evidence suggests that the differences between pairs of lines was slight and that the lower line of a pair could not contribute anything to the higher line. Thus any loss which occurred during selection probably occurred in the random-mated lines, though the possibility that the A lines obtained wider samples from the base population cannot be checked except by more replication. Evidence from crosses between the lines suggested strongly that the differences between the lines were due to recessive genes in the higher line. Thus assortative mating may have been more effective in raising the frequency of rare recessive genes with small effects.

The difference between the results obtained from the O lines and those from the F and D lines may have arisen because of the difference between their base population treatments. The O lines were drawn from a randomly mated line (10 pairs per generation) which had been mated on a rotational basis to limit inbreeding. The rotation had been upset slightly because an attempt was being made to keep its pedigree structure identical with that of two other lines run concurrently. Nevertheless nine of the families had reached the same level of inbreeding, 9.375%, and one was 7.81%. The coefficients of relationship between the families formed a graded series

from zero to 0.3125, except in one case when it reached 0.156.

When the matings were made in generation zero, an attempt was made to equalise the selection differentials, to use flies from each O line from each family and, where possible, to use the same combinations of parentage, though the limitations of the mating systems rendered this ineffective. The result in generation 1 was a series of families with the following range of inbreeding coefficients (percentages).

ASO - 0.0, 0.0, 0.0, 0.0, 0.0, 2.3, 3.1, 4.7, 4.7, 10.9%

RSO - 0.0, 0.4, 0.4, 0.4, 3.1, 4.7, 4.7, 10.9, 10.9%

It can be seen that the range of inbreeding coefficients of the families is highly variable. The extremely high scoring family which arose in RSO generation 1 (mean score 38.57 chaetae) had an inbreeding coefficient of 4.7% and a mean score of 43.5 chaetae. It had three families of double first cousins, one in RSO with 40.15 chaetae and two in ASO generation 1 (mean score 39.23 chaetae) with scores of 39.85 and 39.55. The contribution made by this high family in generation 1 reached 67.5% of the genes in RSO generation 5.

It does not seem unreasonable to attribute the different behaviour of the O lines to this inbreeding effect in the base population.

The evidence on the effectiveness of family selection is in line with the theoretical expectation of an increased response of 7.5% under random mating. The actual increase in response in the random mated line with index selection was 11.1% compared with RSD and 35.3% compared with RSO at generation 5. The equivalent increases in assortatively mated lines were 26.5% and 36.4% respectively. No theoretical estimate is possible for the assortatively mated comparisons, though it is of significance that

the superiority of index selection was greater with assortative mating.

When the inbreeding of the base population is taken into account, the response in RSO should theoretically have been 93% of that in RSD; it was in fact only 82% at generation 5. Because of this, there was an abnormally large difference between RFIS and RSO.

Considering the inbreeding of RSO, index selection in RFIS would theoretically be responsible for a 13% increase in response over RSO. At generation 5 the observed increment was 35%.

Nevertheless, the agreement between these observed and expected values is reasonably good when one considers that the design of the experiment was such that only the A versus R comparisons were unaffected by base population samples. The O, D and F base populations were sampled from the Kaduna cage at different times. Even if they had been sampled simultaneously, the fact that they were subject to an average inbreeding of 17.6% at generation 5 would have meant that the standard deviation of line means at generation 5 due to genetic drift alone would have been 0.873 chaetae ($2F\sigma_G^2$). Though the experimental lines were sampled in pairs, the actual standard deviation between line means at generation 5 was 4.11 chaetae. These values suggest that the deviations of the differences from expected in the index individual selection comparisons is slight; further, the probability of the differences arising from chance alone is negligible.

The general implications of this work for animal breeding are considerable. The so-called aids to selection in animal breeding are mainly variations of family selection, family-, progeny-, sib- and ancestor-selection. These all became relatively more effective in improving the response to selection as the heritability decreases.

Assortative mating, on the other hand, becomes more effective as heritability rises, because of its dependance on m which equals $r_{SD} h^2$.

Since the normal aids to selection increase h^2 they can all increase the effectiveness of assortative mating even with high heritability characters.

In recent years there has been a growing realisation that, as a generalisation, characters fall into a spectrum from high to low heritability.

At the high heritability end of the spectrum we expect, beside a rapid response to selection, very little non-additive genetic variation, no inbreeding depression and no heterosis in crosses. Abdominal chaeta score in Drosophila is an excellent example of such a character. At the low heritability end of the spectrum, we generally expect poor responses to selection, inbreeding depression, heterosis in crosses and a marked sensitivity to environmental conditions. Other characters are intermediate in these features. The general tendency is that the high heritability characters are not closely related to reproductive fitness, or may have some intermediate optimum, while the characters more directly concerned with reproductive fitness are mostly of the low heritability type. When we select artificially, we do no more than to add another component to the general fitness syndrome of our experimental animal. The general finding is that the high heritability characters tend to move towards the low heritability type under selection, though no-one has yet demonstrated inbreeding depression and heterosis in characters which were originally of the high heritability type. This may merely reflect the different time scale of selection experiments from that of evolution.

However, one evolutionary consideration of the general finding that characters tend to respond to selection for only a relatively short period before reaching a plateau seems to have been overlooked.

If a species is in equilibrium with its environment and then conditions change rapidly, probably a number of characters which allow better adaptation come under selection simultaneously. The amount of selection each receives

is related to its phenotypic variability and adaptive value. The result, as far as the species is concerned, is more complex because adaptation also depends upon the response to selection, i.e. the heritability, and the level of the plateau possible from the base population available. Furthermore, at plateau many characters - or even the same character under different circumstances - may show extremely high variability; and this will allow a proportionately higher fraction of the available selection differential to be dissipated. Thus, if the species is not adapted to the new conditions at this stage, its ability to compete interspecifically is lowered. The consideration of selection responses and limits for the different types of character is therefore important from the evolutionary as well as the animal breeding or artificial evolutionary point of view.

Both in animal breeding and rapid evolution, the high heritability characters are of considerable importance for in both one would expect appreciable changes to accrue from selection in fitness or low heritability characters only after recent crosses between diverse strains.

In animal breeding the problem of rapid response and maximum plateau is just as important as in natural evolution. For any character, those two aspects of selection are related to the base population and the amount of subdivision of the selection practised. In animal breeding the current emphasis on pure breeds and closed populations is likely to be quite undesirable, particularly for low heritability characters. For high heritability characters it is often assumed that mass selection is adequate, since the available aids to selection give such a small improvement in selection response that the operational problems associated with their use are not justified.

In the experiments described above, using a typical high heritability character, the greatest effect was obtained by the use of assortative mating with a conventional animal breeding technique. In low heritability characters

the response is likely to be less but since conventional animal breeding techniques are more commonly used here, and the additional use of assortative mating presents no operational problems and is likely to give some extra selection response. In such characters one might also recommend the use of regular crossing followed by periods of aided selection and assortative mating based on the aid used.

Another aspect of animal breeding is the current emphasis on the size of the selection operation. The evidence presented here for an intensity of selection comparable to the average of male and female selection intensities obtained with most domestic animal species suggests that the effective population is very considerably less than the actual size. Further, under conditions of high heritability (high between-family variance) and intense selection, this is necessarily so. Since under these conditions chance loss of genetic material becomes more probable, the use of replication - both within and between base population samples - is probably desirable.

In animal breeding one might consider the problem involved as one of adequately sampling the population, which may include the whole species, to ensure that all useful genes enter the improved population. Thereafter, crosses would be made (probably assortatively) to limit the number of lines for selection with assortative mating. After a few generations one might expect the response to selection to be falling off, so that selected lines would again be crossed assortatively to increase response by utilising the between-line variation. This between-line variance would be readily usable immediately after a cross, since genes differing in the two lines would be at a gene frequency of 0.5.

In an overall scheme of this type one can visualise the most effective use of assortative mating. Such a scheme would allow a greater selection response to be obtained yet would continually replace the genetic variation

lost as a result of the greater inbreeding involved with efficient assortation genetically.

VI. Summary and Conclusions

In the absence of a theoretical examination of the effectiveness of assortative mating with selection, an experiment was carried out to compare assortative with random mating in lines selected for high abdominal chaeta score in Drosophila melanogaster.

Three paired replicates were made; two involved selection and mating based on individual phenotypes and in the third selection and assortative mating was based on an index of weighted family mean and individual phenotype. The index was used to allow a more accurate selection and assortative mating genetically.

The intensity of selection in all lines was one in ten.

Comparisons were possible between assortative and random mating with selection and between index and individual selection.

In all cases assortative mating gave a greater response to selection and this was partly due to a greater realised heritability and in two replicates to a greater selection differential.

In two replicates the rate of inbreeding was greater under assortative mating than with random mating. The highest rate of inbreeding was achieved with a combination of assortative mating and index selection, though the index-selected lines were twice the actual size of the mass-selected lines. This is in accordance with the proposition that the rate of inbreeding during selection is related to the variation between families and the intensity of selection (constant in these comparisons), since the between-family (and total) variation was consistently higher in the assortatively mated lines than under random mating.

Index selection with random mating gave an increased response to

selection, and this increased response was of the order expected from theoretical considerations. The difference between assortative and random mating was greater with index selection and assortative mating than when selection and assortative mating were based on individual phenotypes. This appeared to be due to the more accurate assortment of mates genetically.

It is suggested that assortative mating is a method of obtaining an increased response in selective animal breeding. Its particular characteristic is that it becomes a more powerful tool under conditions of high heritability, whereas all of the conventional aids to selection used in animal breeding become relatively more effective under low-heritability conditions. The use of these conventional aids to selection in conjunction with assortative mating is likely to be justified under high heritability conditions, since they allow a more accurate assortment of mates genetically.

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FIGURES

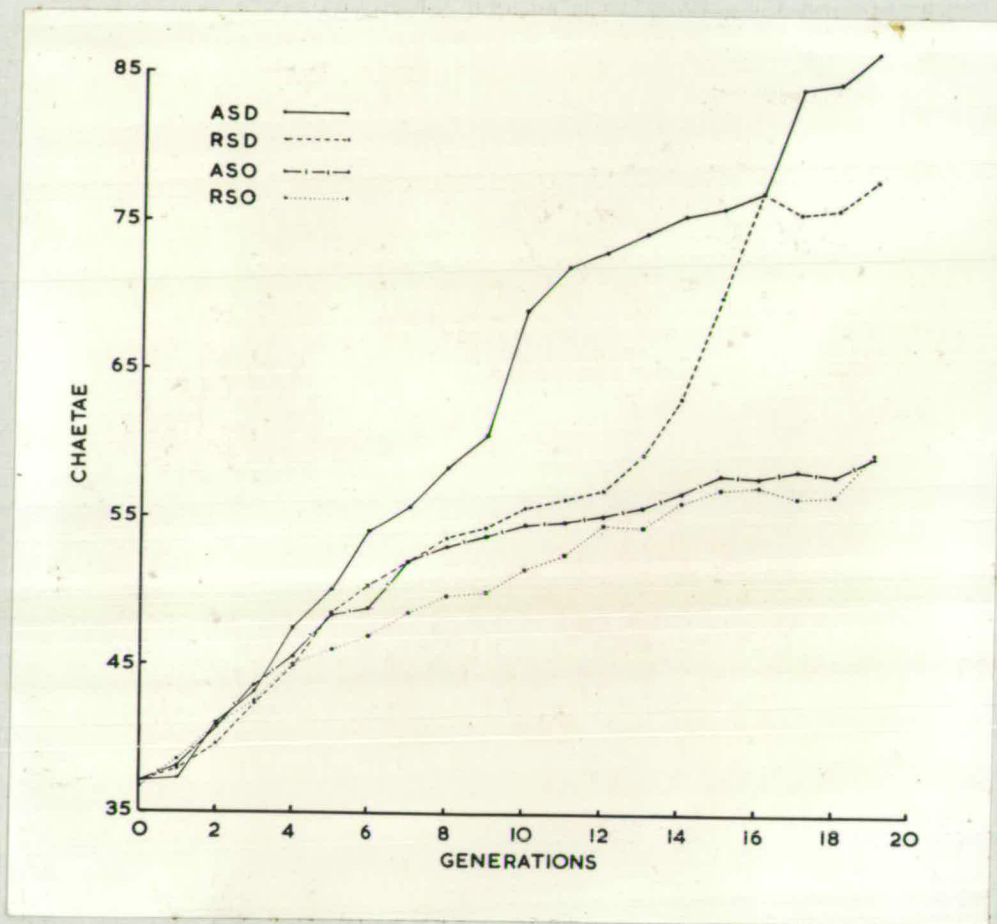


Figure 1. Response to individual selection over 19 generations. Selection intensity 10/100 of each sex. Generation means based on average of male and female scores.

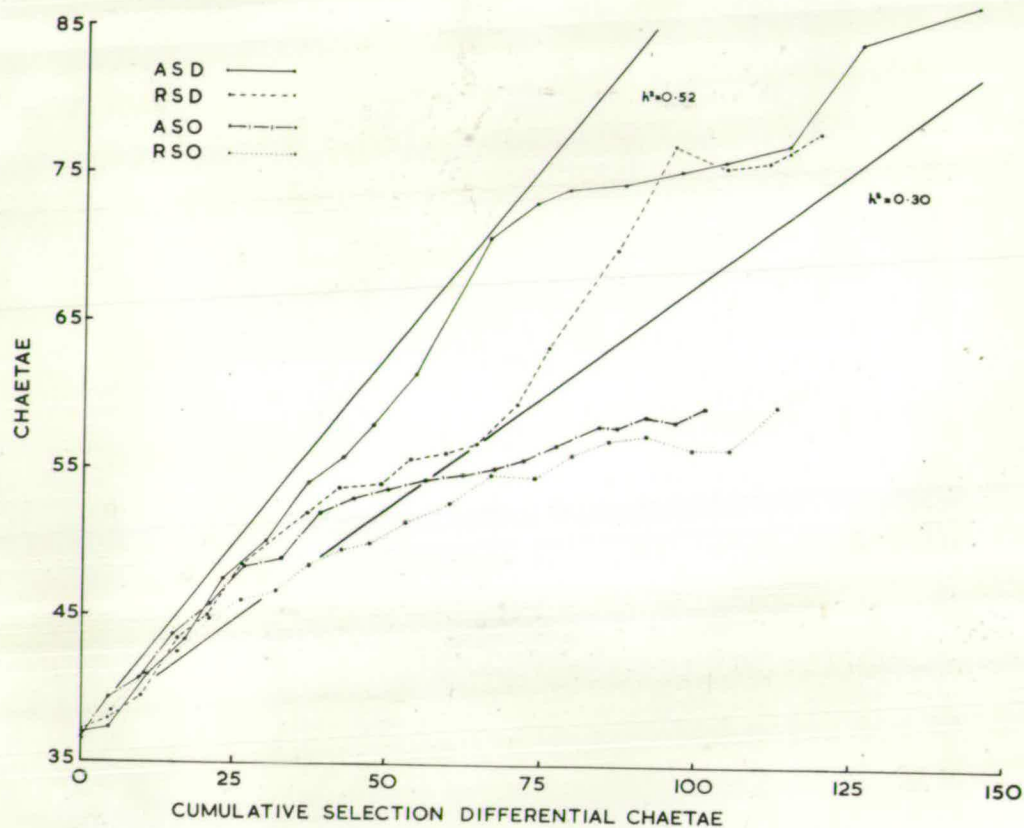


Figure 2. The relationship between response to individual selection (as in Figure 1) and the cumulative selection differential applied. The slope of the line at any generation is an indication of the realised heritability.

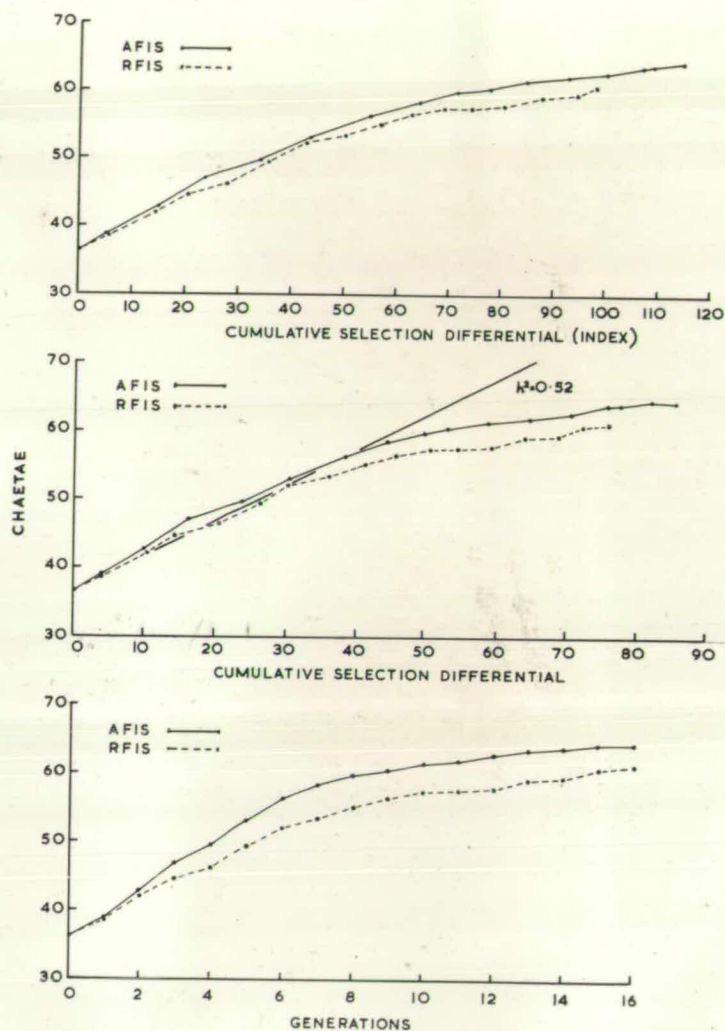


Figure 3. Top. The relationship between the response to index selection of 20/200 of each sex and the cumulative index selection differential applied. Centre. As for the top graph except that the cumulative selection differential is expressed in terms of phenotypic means. Bottom. The response to index selection over 16 generations.

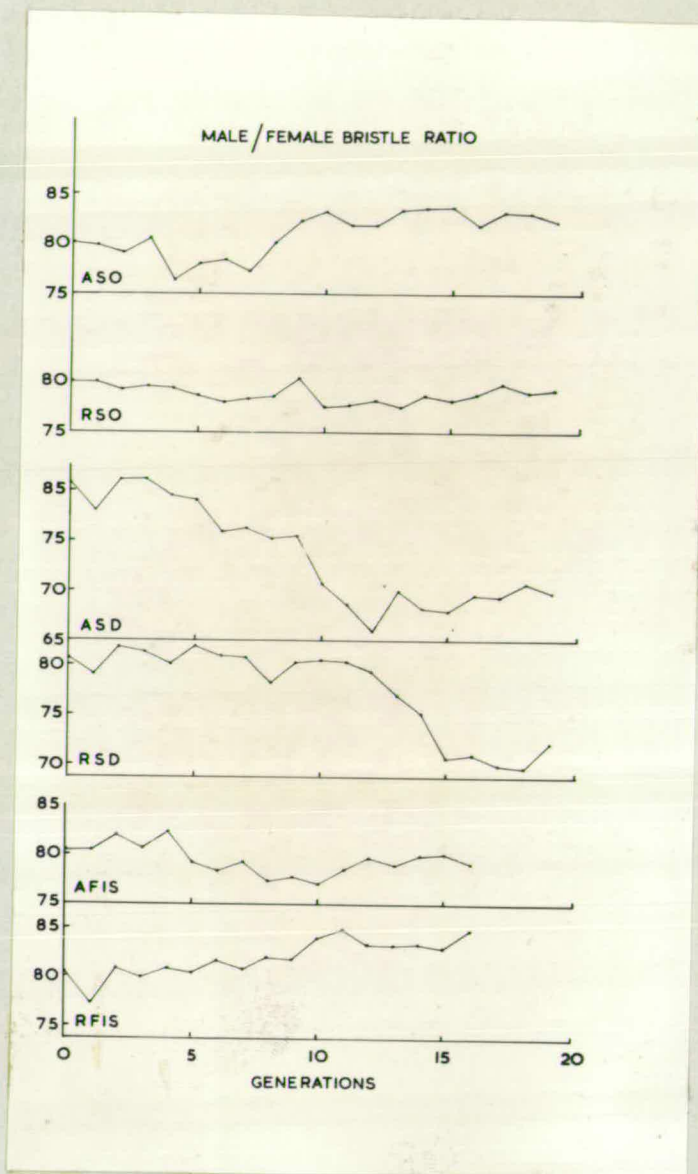


Figure 4. The male/female chacta score ratios for the six lines for each generation.

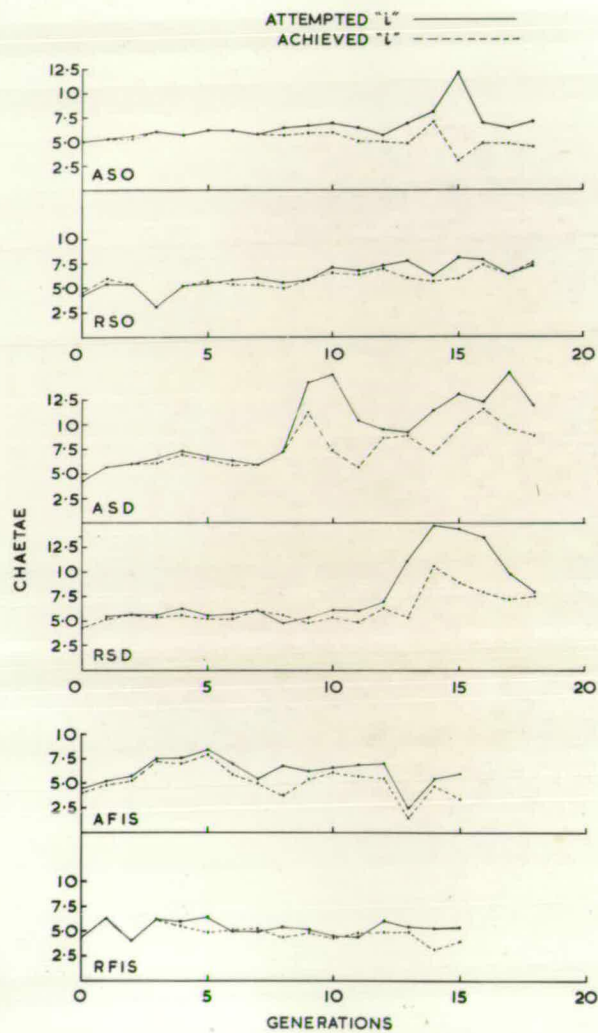


Figure 5. The attempted and achieved selection differentials in each generation for each line. The differences between the two was brought about by losses of matings.

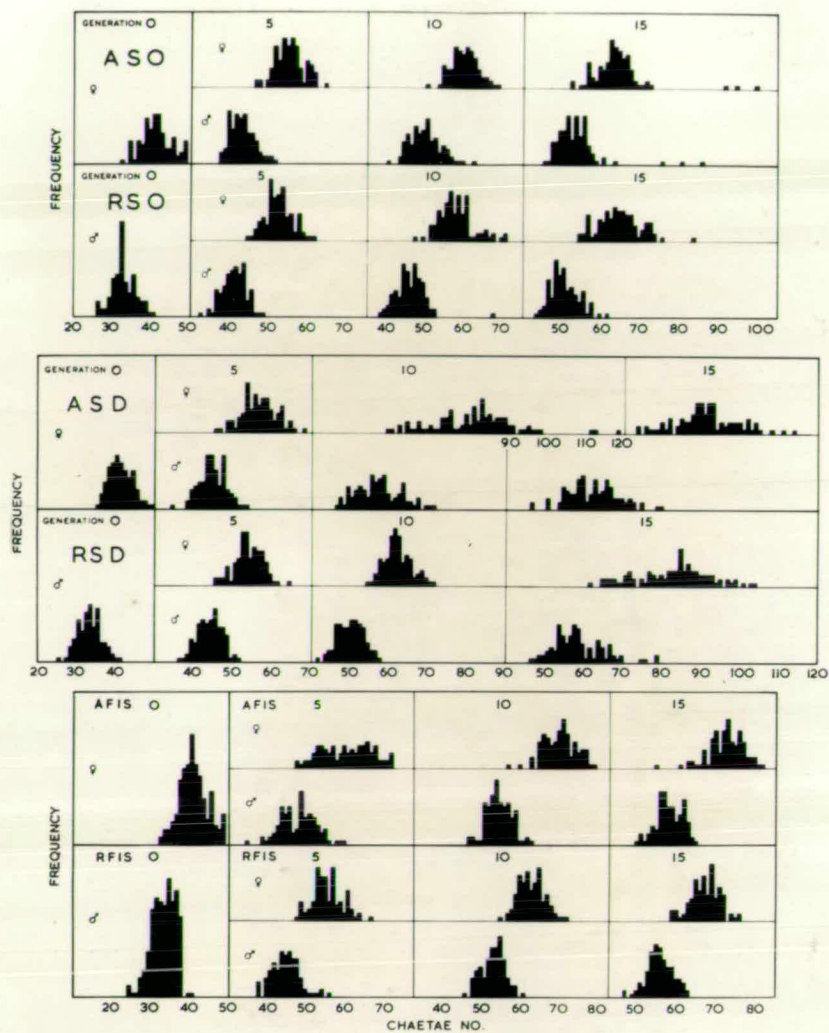


Figure 6. Frequency histograms for chaetae score in each sex for the three base populations and the six lines at generations 5, 10 and 15.

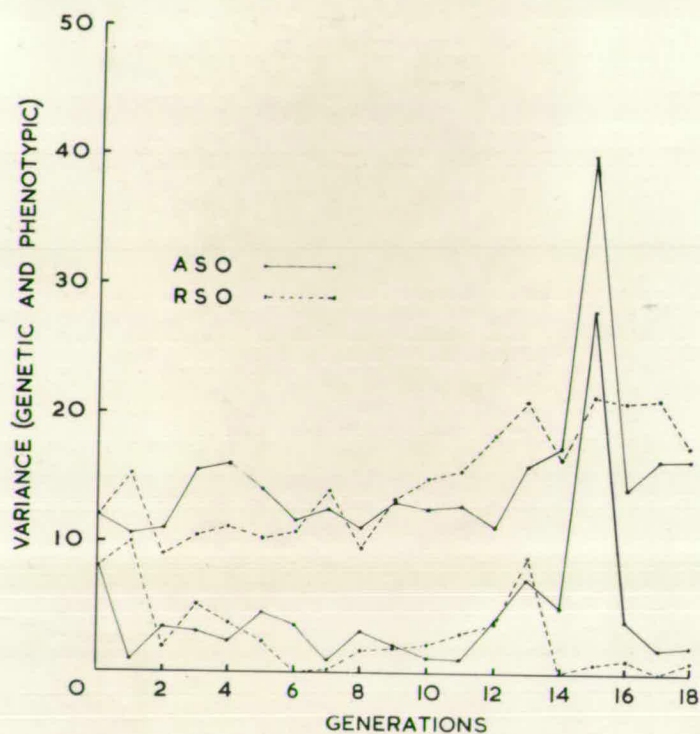


Figure 7. Phenotypic and genetic (twice the between-family variance component) variance for each generation in the O lines.

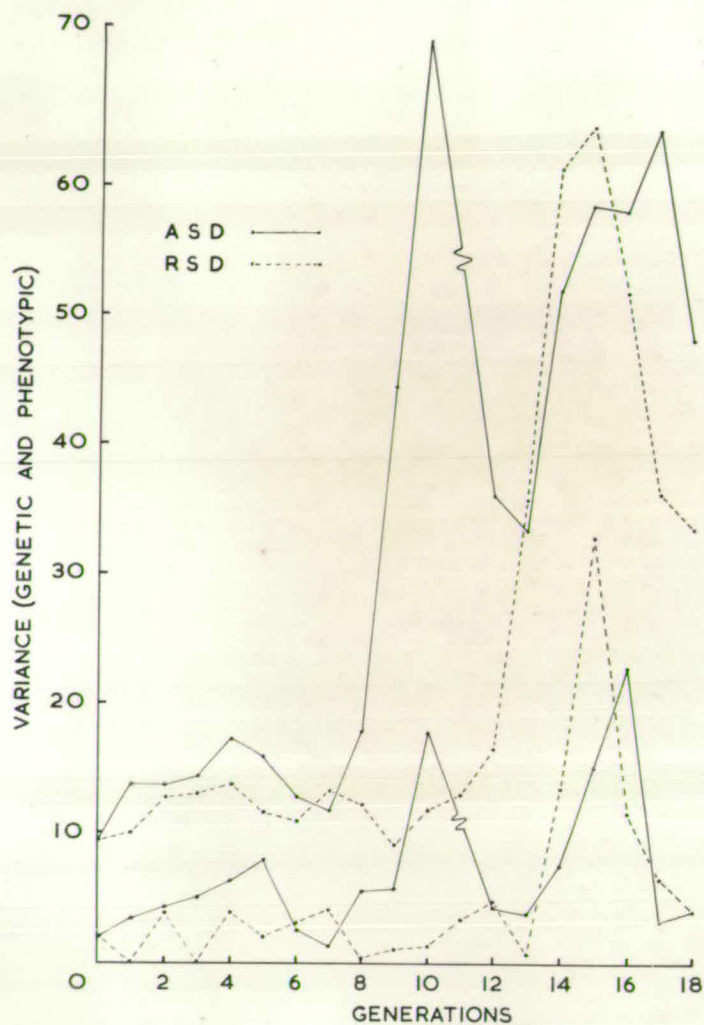


Figure 8. Phenotypic and genetic (twice the between-family variance component) variance for each generation in the D lines.

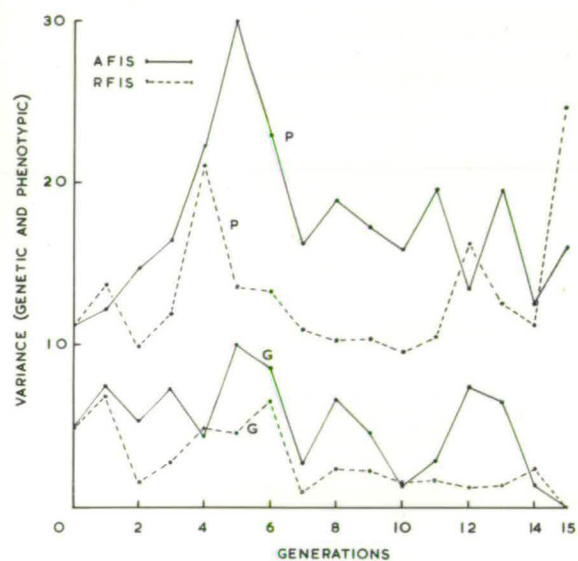


Figure 9. Phenotypic and genetic (twice the between-family variance component) variance for each generation in the F lines.

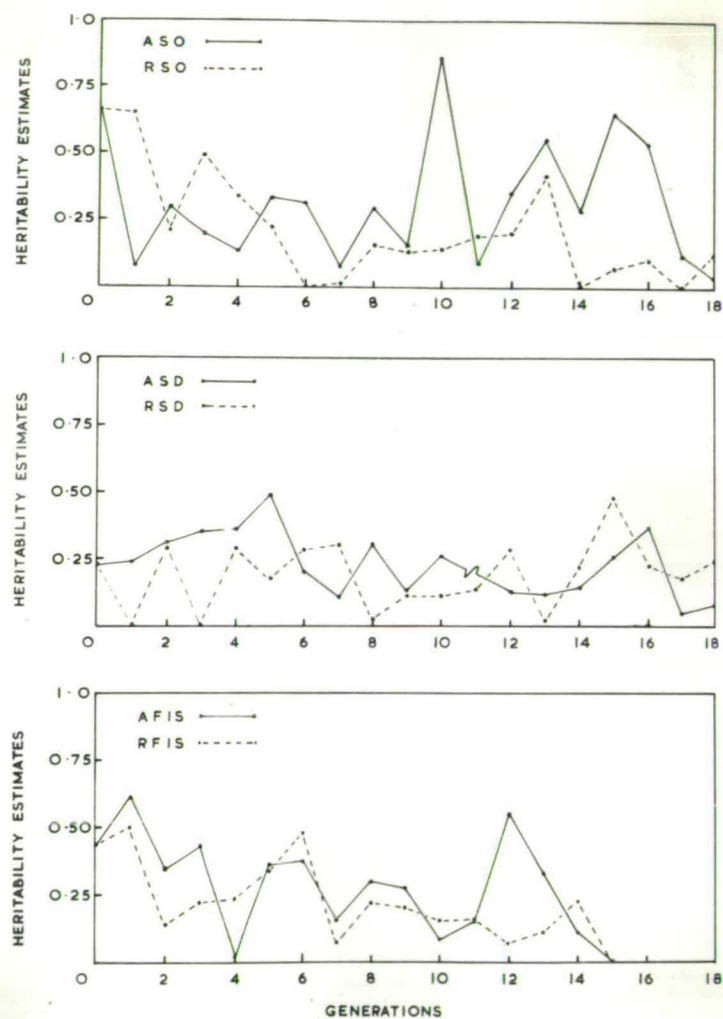


Figure 10. Heritability values for each generation in each line. The heritability values based on the genetic and phenotypic variances in Figures 7, 8 and 9.

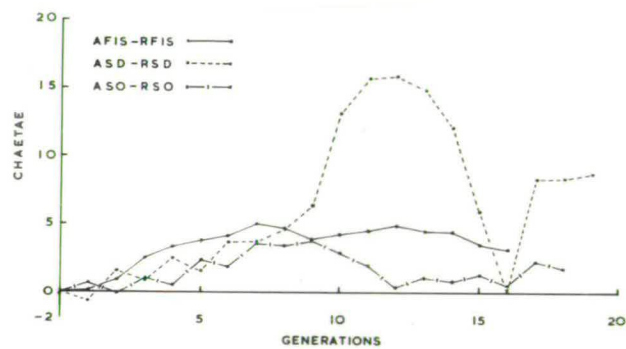


Figure 11. The differences between assortatively and random mated lines in each generation based on the generation means shown in Figures 1 and 3.

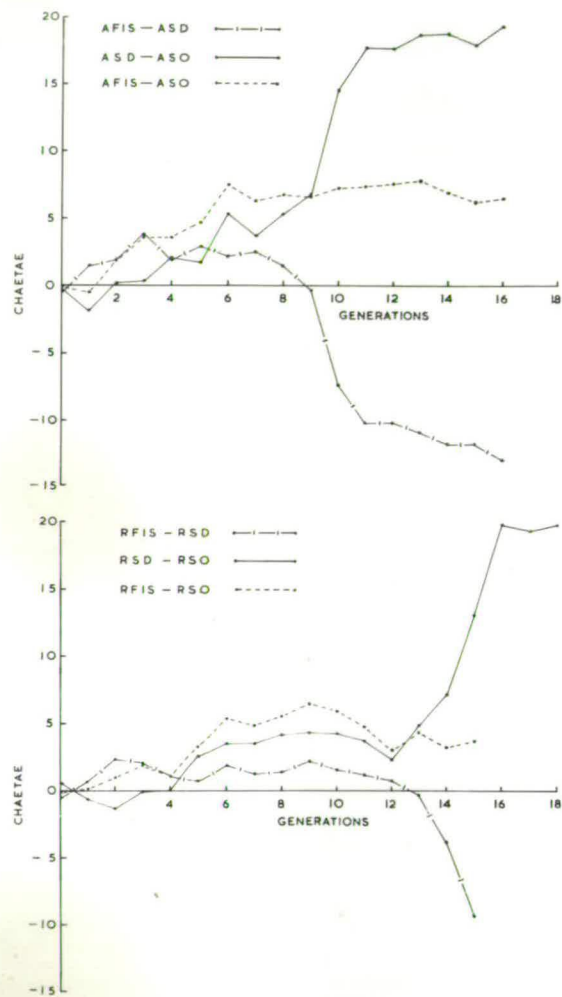


Figure 12. Top. Differences between assortatively mated lines.
Bottom. Differences between random mated lines.
 (Data from Figures 1 and 3).

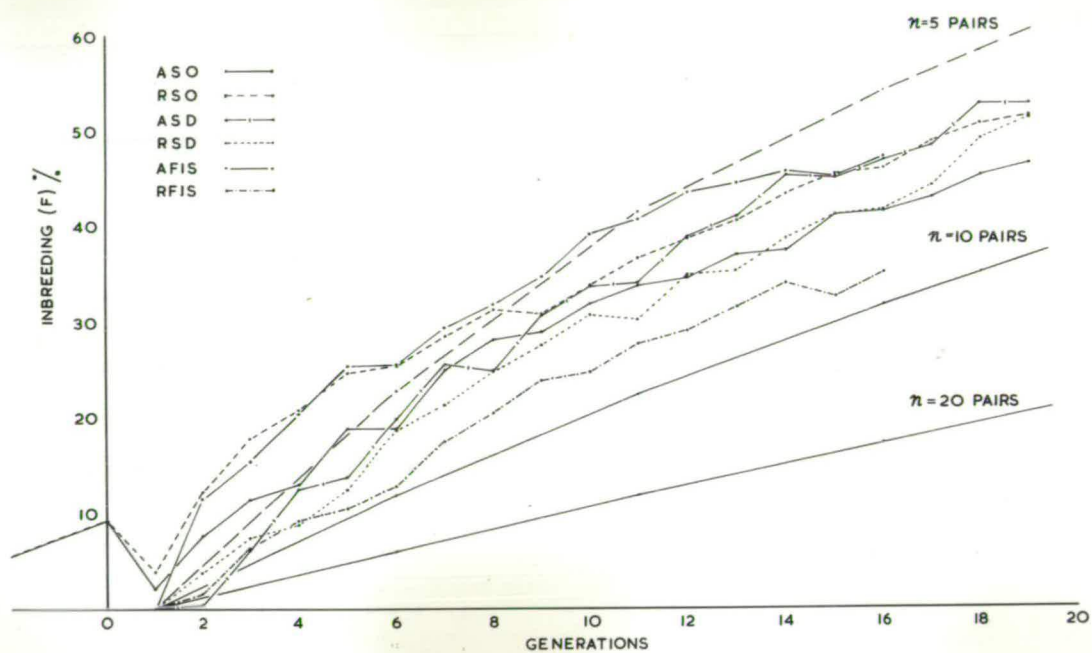


Figure 13. Average inbreeding coefficients for each generation in each line.

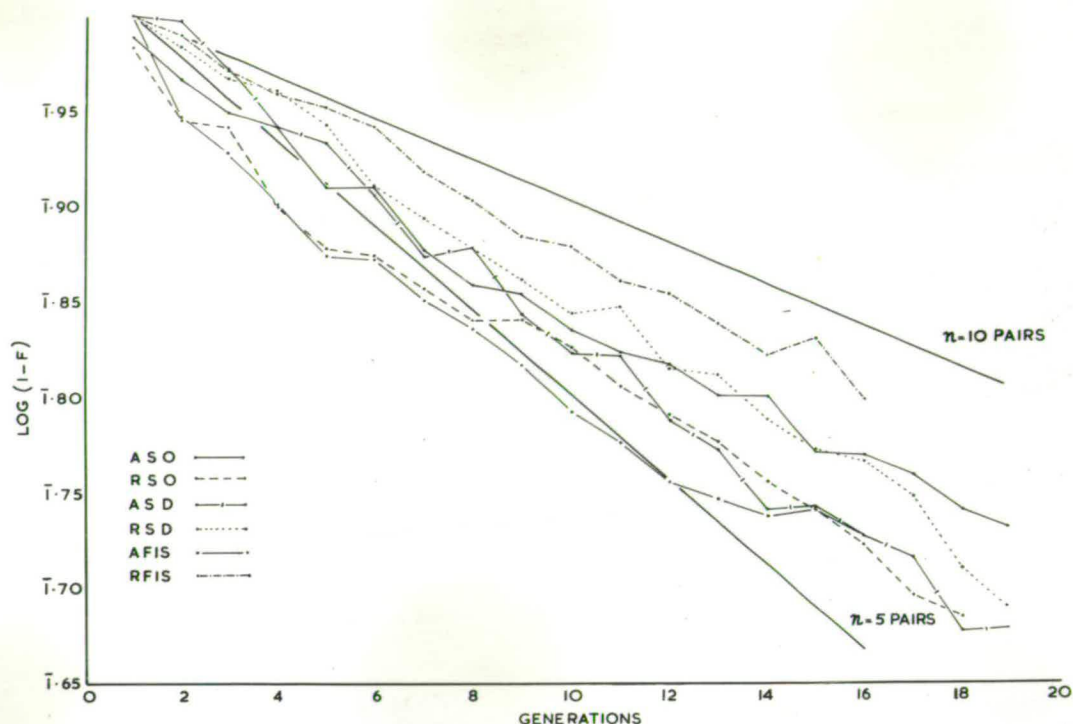


Figure 14. Log (1-F) values for each generation in each line.

\bar{F} is the average inbreeding coefficient shown in Figure 13. (1-F) indicates the expected genetic variability remaining in the lines. The slope of the curves gives an indication of the effective population size at any generation, thus curvilinear regressions mean that the effective population size changed throughout the experiment.

The values of the regression coefficients are shown below, all are highly significant.

ASO	b_1	=	-0.0141	(equivalent to a rate of inbreeding of 3.2% per generation)
	b_2	=	0.0003	
RSO	b	=	-0.0151	(" " " " " 3.4% " ")
ASD	b	=	-0.0186	(" " " " " 4.2% " ")
RSD	b	=	-0.0163	(" " " " " 3.2% " ")
AFIS	b_1	=	-0.0161	(" " " " " 3.6% " ")
	b_2	=	0.00020	
RFIS	b	=	-0.0133	(" " " " " 3.0% " ")

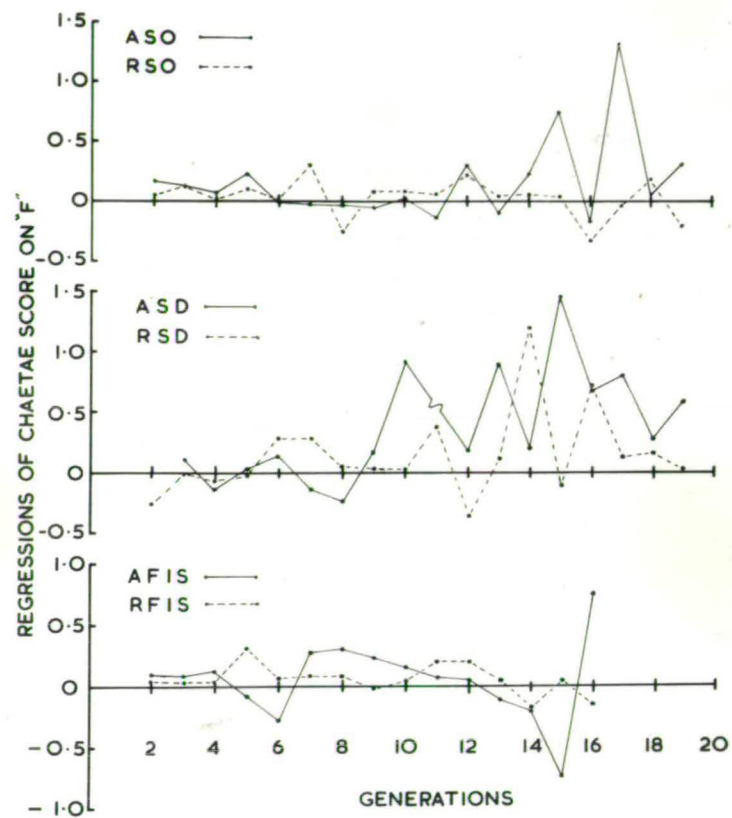


Figure 15. Top. Regressions of mean family chaetae score on family inbreeding coefficient expressed as a percentage for each generation in lines ASO and RSO. Centre. As above for lines ASD and RSD.